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# Do red deer hinds prefer stags that produce harsh roars in mate choice contexts?

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## Keywords

red deer; female mating preferences; vocal communication; nonlinear phenomena; playback experiment.

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## Abstract

Red deer stags give two types of roars during the breeding season, termed 'common' and 'harsh' roars. This study tested the hypothesis that the characteristic spectro-temporal structure of male harsh roars functions to directly attract females towards male callers during the breeding season. The results show that oestrous hinds look for longer towards speakers broadcasting sequences containing harsh roars, but do not preferentially approach or spend more time in close proximity to speakers broadcasting harsh roars over those broadcasting only common roars. While these observations confirm that the specific acoustic structure of male harsh roars functions to draw the attention of hinds, they are not consistent with the notion that these calls have an immediate impact on mate choice decisions by stimulating oestrous hinds to move towards male callers. Consequently, we suggest that intersexual selection through female mate choice is unlikely to be a major factor driving the evolution of male red deer harsh roars.

## Introduction

Mating is accompanied by song and other acoustic signals in many animal species and such signals are generally assumed to be under strong pressure by sexual selection (Andersson, 1994). The relative importance of intra- and intersexual selection in shaping the evolution of male traits, however, can often be hard to determine (Charlton, 2013). In general, this lack of evidence stems from the confounding influence of intense male competition for access to females. In addition, demonstrating female preferences for specific male traits correlated with mating success requires other aspects of the male phenotype to be experimentally controlled for. Acoustic signals are one such aspect of the male phenotype that can be accurately reproduced in the absence of other male stimuli, and some of the best evidence so far for female preferences has been acquired using playback experiments (e.g. Catchpole, 2000; Charlton *et al.*, 2012; Gerhardt, 1991; Ballentine, Hyman & Nowicki, 2004; Scheuber, Jacot & Brinkhof, 2004; Pasch *et al.*, 2011).

The involvement of vocal communication in mammalian reproduction has been studied most thoroughly in red deer (for an overview see Reby & McComb, 2003b). Playback

experiments on female red deer have shown that hinds are more likely to look at and approach speakers playing male common roars delivered at higher rates during the breeding season (McComb, 1991). More recent playback work on oestrous hinds has revealed a mating preference for males that produce roars with lower formant frequencies simulating larger callers (Charlton, Reby & McComb, 2007) and higher fundamental frequencies (Reby *et al.*, 2010). Red deer stags also produce 'harsh roars' in situations of intense activity such as after a roaring contest or during a period of repeated herding (Reby & McComb, 2003b; Reby *et al.*, 2005), which are defined by a chaotic source (non-linear phenomena) as well as a staccato time structure and lower formant frequencies corresponding to a fully extended vocal tract (Reby & McComb, 2003a). Harsh roars appear to be important during intrasexual competition (Reby *et al.*, 2005), but they also trigger stronger reactions in hinds than common roars, as well as increasing their attention to subsequent common roars from the same stag (Reby & Charlton, 2012). Whether male red deer harsh roars also function to attract oestrous hinds during the breeding season, however, remains unknown.

Because the harsh roars of red deer stags are characterized by broadband frequency noise and are produced with a fully

extended vocal tract (Reby & McComb, 2003a), they typically have more salient and lower formants than common roars, a feature that may make them more attractive to hinds (Charlton *et al.*, 2007; Charlton, Reby & McComb, 2008). Furthermore, the production of harsh roars is characteristic of escalation phases in roaring contests and, therefore, likely to signal a highly motivated caller in good condition (Reby & McComb, 2003a). Consequently, oestrous hinds could potentially gain the direct fitness benefits of greater protection from harassment by joining the harems of these individuals that should be more adept at warding off the reproductive attempts of other stags. In the current study, in order to test the immediate effect of harsh roars on mating choice, we investigate whether oestrous red deer hinds are more attracted to an unfamiliar stag producing both common and harsh roars than to one producing only common roars. We predict that hinds will preferentially approach and spend more time in close proximity to speakers broadcasting playback sequences containing both common and harsh roars than those broadcasting playback sequences of common roars only.

## Materials and methods

### Study site and animals

The research was conducted at the Réserve de la Haute Touche, Muséum National d'Histoire Naturelle, 36 290 Obterre, France, during the 2011 breeding season. We tested 21 red deer hinds (of Scottish origin) aged between 10 and 15 years (mean = 12.6).

### Experimental protocol to control hind hormonal status

Because female mating preferences often only emerge during oestrus (Charlton, 2013), ovulation was controlled and synchronized during the experiment using intravaginal sponges. These intravaginal sponges (2 × 45 mg, Intervet, Angers, France) provide a steady and continuous release of progesterone in order to inhibit normal follicular growth and subsequent release of oestradiol. The sponges were removed after 12–15 days and a 400 UI injection of Pregnant Mare Serum Gonadotropin (Intervet, Angers, France) given to each of the hinds. The playback experiments were performed 35 h later when the hinds came into oestrus.

### Playback stimuli

The bouts of common roars and harsh roars used to construct the playback sequences originated from four farmed adult red deer stags of Scottish origin recorded by DR in France in 1996 and in New Zealand in 2001. Recordings were made with Sennheiser MKH 816 and MKH 416 microphones (Sennheiser, Wedermark, Germany) linked to a Uher 4200 Report Monitor open reel (Uher, Munich, Germany), a Marantz CP 230 cassette recorder (Marantz, Kanagawa,

Japan) or a HHB PDR 1000 professional DAT recorder (HHB, London, UK). Recordings were captured or digitized at 44.1 kHz sampling rate and 16 bits amplitude resolution.

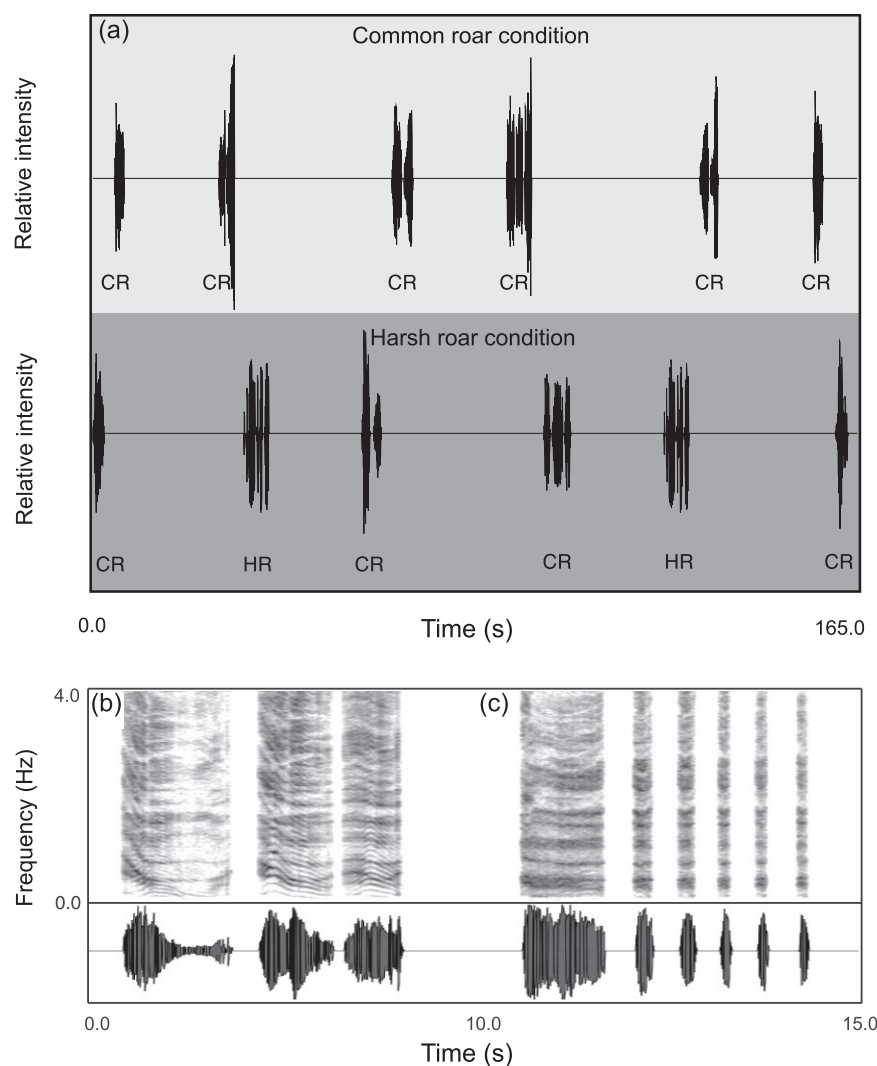
### Playback sequences

The playback sequences consisted of six bouts of roars originating from each of two different stags representing the two different experimental conditions. Roar bouts from each stag exemplar were arranged into six matched pair sequences (Fig. 1). In each matched pair, a bout of roars from one of the two stags was followed two seconds later by a bout of roars from the other stag (*sensu* Charlton *et al.*, 2007, 2012). The next matched pair followed 20 s later, but this time the stag exemplar used to initiate the vocal exchange was alternated (Fig. 1). This allowed us to control for any preferences for bout leaders (previously documented in red deer by McComb (1991)). A common roar and a harsh roar condition were created for each stag exemplar: the common roar condition consisted of common roars only, whereas the harsh roar condition had the second and fifth common roar bouts replaced with harsh roar bouts from the same stag exemplar (Fig. 1). This allowed us to balance the presentation of harsh roars across the sequence for the harsh roar condition while reflecting the natural pattern of red deer roaring, in which harsh roars are interspersed between the more frequently produced common roars (Reby & McComb, 2003b).

In total, hinds were presented with six matched choices between the two conditions over the duration of each playback (approximately 160 s). In order to preserve the natural variability of common and harsh roar bouts, we did not attempt to standardize bout duration or any other spectral parameters. In addition, to limit the possibility of differential behaviour occurring because of differences in the acoustic structure of common roars, we used the same common roars at positions 1, 3, 4 and 6 for each playback condition, thereby ensuring that the only difference between the harsh roar condition and the common roar only condition was the replacement of the second and fifth common roars with two harsh roars. The mean intensity of all bouts was normalized to 99% peak amplitude using the 'scale intensity' command in Praat 5.1.32 (<http://www.praat.org>).

### Playback experiments

The playback experiments were conducted in the mornings between 0900 and 1200 h. In order to simulate a natural vocal interaction between two rutting males (and hence, a realistic mate choice scenario), we used an experimental setup in which each of the two playback conditions were broadcast from two separate speakers (McComb, 1991; Charlton *et al.*, 2007, 2012; Reby *et al.*, 2010). This type of 'two-speaker choice' experimental setup has previously been used in this species to reveal clear female mate choice decisions based on male vocal stimuli (Charlton *et al.*, 2007; Reby *et al.*, 2010; Wyman *et al.*, 2011). The experimental condition played from each speaker and the exemplars used to simulate these conditions were randomized across playback trials to control for any



**Figure 1** Structure of the playback sequences. (a) The structure of the playback sequences was designed to simulate a vocal exchange between two different stags. The harsh roar condition is in dark grey, the common roar condition in light grey: CR, common roar bout; HR, harsh roar bout. The lower panel shows spectrograms of a bout of male common roars (b) and a bout of male harsh roars (c). Spectrogram settings: FFT method, window length = 0.05 s, Gaussian window shape.

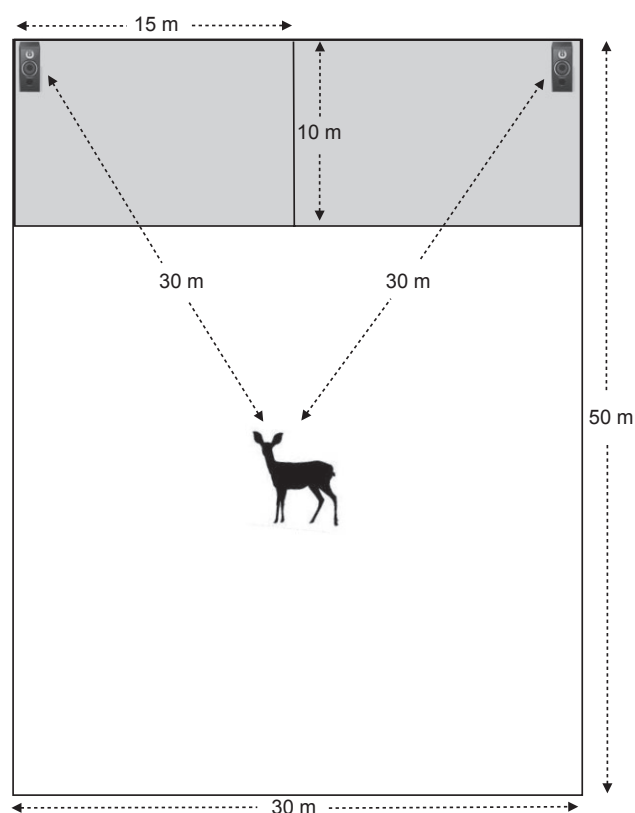
preferences for areas of the experimental site or particular exemplars. The playback stimuli were presented to hinds using two Anchor Audio Liberty 6000HIC loudspeakers (Anchor Audio, Carlsbad, CA, USA) connected by coaxial cable to an Apple MacBook laptop computer (Apple, Cupertino, CA, USA) and placed at a height of 1.5 m from the ground. Roars were broadcast at equal sound pressure levels (105 dB peak sound pressure level at 1 m from the source, determined using a Radio Shack Sound Level Meter (Radio Shack, Fort Worth TX, USA), set for C-weighted fast response).

Each hind was introduced to a rectangular-shaped enclosure (50 × 30 m) with the playback speakers located in the bottom left and right hand corners approximately 30 m from the hind's position at the start of each playback sequence (Fig. 2). Grain was placed on the ground in a central position to ensure that the hinds would be in a standardized context and position at playback onset. The playbacks were initiated when hinds were centrally positioned and their attention was directed away from the speaker positions. A Sony HDR-

TG3E digital video camera (Sony, Tokyo, Japan) mounted on a tripod was used to capture behavioural responses throughout the playback sequences and for 2 min after each playback experimental period. The researchers, computer and video camera equipment were all hidden from the hinds.

### Behavioural analysis

Video sequences were analysed frame-by-frame (frame = 0.04 s) using Gamebreaker 7.0.121 (SportsTec, Sydney, Australia). We measured the duration of each look given towards either of the speaker positions while stationary and the amount of time spent in each side of a 'mate choice zone' leading to either speaker position (Fig. 2). We also noted the first mate choice zone the hind entered and the amount of times they entered either of the mate choice zones (Wyman *et al.*, 2011). Looking was defined as starting when the hind raised or turned her head towards the speaker, having previously faced down or away, and ended when the head moved



**Figure 2** The experimental set up. At playback onset the hinds ( $n = 21$ ) were placed individually in the middle of the experimental enclosure approximately 30 m away from either of the speaker positions. The mate choice zone was located at the end of the experimental enclosure, began 10 m from the enclosure wall, and was split into two sections leading towards either speaker position.

away from the playback source. Entering a proximity zone was defined as starting when the female's entire body had crossed the outer plane of the zone boundary, and ending when the first leg passes out of the zone boundary.

### Statistical analyses

Log (10) transformations were used to normalize the data distribution for the amount of time spent in each mate choice zone and the amount of times hinds entered each of the mate choice zones. To retain zeros in the dataset, a value of one was added to each data point before transformation. Looking duration was normally distributed (Kolmogorov–Smirnov:  $P > 0.05$ ). Paired  $t$ -tests were used to compare looking duration, the amount of times hinds entered each of the mate choice zones, and the total amount of time spent in each mate choice zone. A binomial test was used to determine whether hinds entered either of the mate choice zones first more often than would be expected by chance. Significance levels were set at  $P = 0.05$  and two-tailed probability values are quoted. All

data analyses were performed with IBM SPSS Statistics v20 (Chicago, IL, USA) for Mac OSX.

### Results

Oestrous red deer hinds spent more time looking towards speakers broadcasting playback sequences containing two harsh roar bouts than they did to playback sequences containing only common roars (Fig. 3a) ( $t_{20} = 3.54$ ,  $P = 0.002$ ). However, they did not enter the mate choice zone of the harsh roar condition first significantly more often than the mate choice zone of the common roar condition (Binomial test:  $n = 10$ ,  $P = 0.344$ ), or enter the mate choice zone of the harsh roar condition more times (Fig. 3b) ( $t_{20} = -1.24$ ,  $P = 0.228$ ). In addition, the amount of time spent in the mate choice zone of the harsh roar versus the common roar only condition did not significantly differ (Fig. 3c) ( $t_{20} = -9.19$ ,  $P = 0.369$ ).

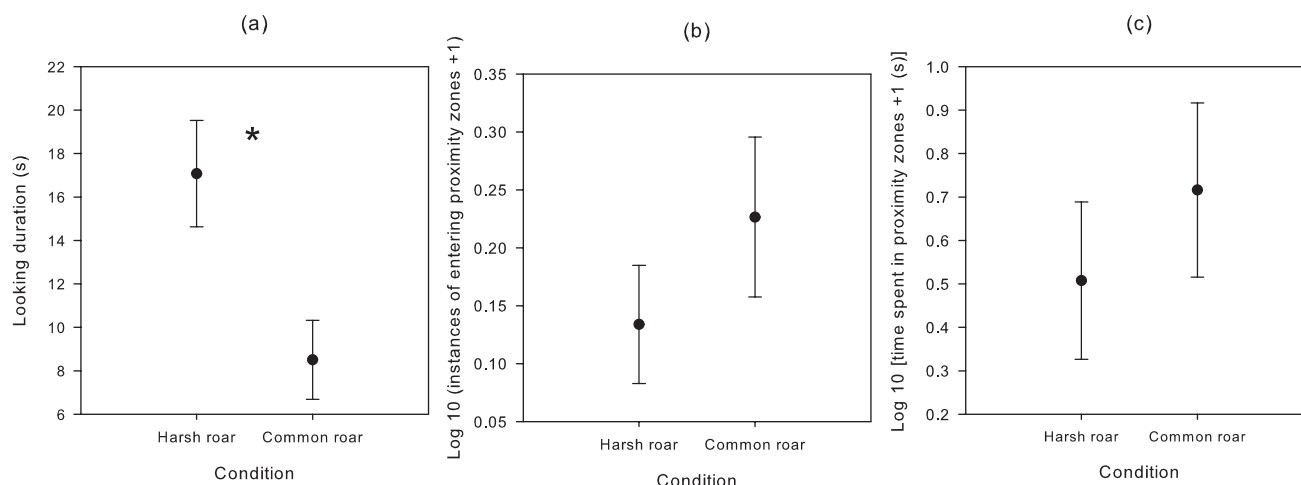
### Discussion

The results of the current study show that red deer hinds in peak oestrus do not preferentially approach, or spend more time in close proximity to speakers broadcasting sequences of common roar bouts interspersed with two bouts of harsh roars over those containing common roar bouts only. In free-ranging conditions, the active approach of an oestrous hind to a stag typically leads to mating (Clutton-Brock, Albon & Guinness, 1982). Consequently, in our experiment, any preferential movement towards either speaker would clearly have been equivalent to a mating choice/decision. Extrapolating to mate choice in the wild the current findings do not suggest an immediate impact of male harsh roars on female mate choice decisions.

Nonetheless, hinds did spend more time looking towards the speaker broadcasting the harsh roar condition than they did to the speaker broadcasting the common roar only condition. Harsh sounding calls often function to recruit attention (Gouzoules, Gouzoules & Marler, 1984; Townsend & Manser, 2011) and previous work has shown that male red deer harsh roars trigger stronger looking responses in hinds than common roars (Reby & Charlton, 2012). Consequently, while the current results indicate that harsh roars do not stimulate oestrous red deer hinds to approach stags any more than common roars do, they are in accordance with our previous findings that suggest harsh roars have an attention-grabbing function during the breeding season (Reby & Charlton, 2012), and this may have a longer-term effect on female mate choice.

Future work should investigate the response of red deer stags to common roar sequences containing harsh roars versus those without. Playbacks of resynthesized common roars simulating different size rivals have shown that male red deer produce more harsh roars when confronted with larger size variants (Reby *et al.*, 2005). These observations suggest that harsh roars are used to broadcast the maximum impression of the caller's body size during intrasexual competition. Indeed, the harsh quality and broadband frequency noise of these calls makes them ideally suited to highlight size-related formant information (Owren & Rendall, 2001; Fitch, Neubauer &





**Figure 3** Results of the playback experiment. Error bar charts show mean  $\pm$  standard error of hind behavioural responses (\* $P < 0.05$ ). (a) Looking responses, (b) the number of times that hinds entered each of the mate choice zones and (c) the time spent in each mate choice zone.

Herzel, 2002; Reby & McComb, 2003a). In addition, the spectro-temporal features of these calls may also communicate information about the caller's motivational state during intrasexual competition (Reby *et al.*, 2005). Furthermore, the different acoustic features of harsh roars may serve different functions, in broadcasting size-related information, the caller's motivational state and for grabbing female attention. Thus, playback studies could also isolate and manipulate different spectro-temporal features of these calls in order to investigate their relative importance in different contexts.

In summary, although our findings indicate that male red deer harsh roars may affect long-term mating decisions (McElligott, O'Neill & Hayden, 1999; Reby *et al.*, 2001), they do not suggest that the specific acoustic structure of these calls functions to directly attract oestrous hinds during the breeding season. These observations suggest that intersexual selection through female mate choice is unlikely to be the main factor driving the evolution of these calls. We suggest instead that male red deer harsh roars evolved primarily to highlight body size-related information during intrasexual competition (Reby & McComb, 2003a,b; Reby *et al.*, 2005), as well as to draw the attention of hinds to male callers during the breeding season (Reby & Charlton, 2012). Further playback studies on male red deer are now required to confirm the intrasexual role of these calls in this species' sexual communication.

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